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COMPOSITION AND RELATIVE ABUNDANCE IN A TEMPERATE ZONE BUTTERFLY FAUNA

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THE DONNER PASS AREA, lying on the crest of the Sierra Nevada range in Placer County, California, provides a rich variety of habitats lying between 6900 and 8300 feet elevation. During the summers of 1956 and 1960, the authors made an intensive study of this region and we have reported elsewhere (Emmel & Emmel, 1962a, 1962b) on the ecology and factors affecting distribution of the 74 species composing the butterfly fauna. We wish to report here the interesting data obtained on the faunal composition and relative abundance of species within the seven major Rhopalocera groups recorded in the Donner Pass area, and to evaluate the possible factors influencing this distribution of species.

INTRODUCTION

Hovanitz (1958) has recorded the occurrence of Rhopalocera families and genera at each five degrees of latitude and 1000 meters of elevation above sea level for the entire New World. However, this study did not include the *numbers* of species or genera in each family that occurred in each of these areas. Tilden (1959) divided the butterflies of the Tioga Pass area under five plant associations; Emmel & Emmel (table 1, 1962a) partitioned the Donner Pass fauna under four plant associations. But these authors did not compare the faunas of each association or attempt to ascribe reasons for the greater number of species of a particular family in one association than another. The purpose of this paper is to report an examination of the composition and habitat associations of the Donner Pass fauna and from this examination to derive some understanding of the factors affecting the distribution and success of species in a butterfly family within a given set of environments.

DESCRIPTION OF STUDY AREA & METHODS

In a previous paper (Emmel & Emmel, 1962a), four general vegetational associations representing the union of floras from three

life zones (Transition, Canadian, and Hudsonian) were delineated, and may be briefly reviewed.

1. The *Wet-Meadow* habitats (elevation 7000-7260 feet) support verdant expanses of grasses (*Poa* species) and sedges (*Carex*), *Lilium, Mimulus, Delphinium, Castilleia,* and other wildflowers, with scattered thickets of willows (*Salix*) along the stream banks. *Trifolium, Viola, Aster, Potentilla,* and other lepidopterous food plants (see table IV) are common.

2. *Dry-Meadow* areas (elevation 6800-7600 feet) are moist in the spring but are dry throughout July and August. Fireweed (*Epilobium angustifolium*), *Achillia, Calyptridium,* and *Penstemon,* as well as grasses, are typical plants. Food plants include *Ribes, Polygonum, Lupinus, Gnaphalium,* and others as listed in table IV.

3. Dense *Forest* (elevation 6800-7600 feet), mainly of Canadian-Zone trees, covers about one-half of the total Pass area. Red Fir (*Abies magnifica*), *Pinus contorta, P. monticola,* and Mountain Hemlock (*Tsuga mertensiana*) represent the majority of the forest trees. Only three known butterfly food-plant genera are found here: *Pinus, Arceuthobium,* and *Ceanothus.*

4. The *Montane* areas (elevation 7160-8383 feet) are generally open talus slopes, where the dry, almost soilless environment discourages the growth of most trees. Included in the flora of these mountain peaks are Rabbit Brush (*Chrysothamnus*), Sage Brush (*Artemisia*), Mule-Ears (*Wyethia mollis*), *Lupinus,* and *Sedum* species. *Eriogonum, Astragalus, Potentilla, Ceanothus,* and other food plants in Table IV, are widely distributed here.

Thus the diversity of vegetational associations in this temperate-zone locality provides habitats and food plants for a considerable number of butterfly species, and it is of interest to compare the relative success of species in different families in colonizing this favorable yet rather small area (six square miles) in the Sierra. In 1956 and 1960, the *number of species* (see Emmel & Emmel, 1962a, for a detailed listing) in each of the four vegetational zones was determined by intensive collecting throughout Donner Pass.

In the course of studying the influence of meteorological conditions on the flight activity of these species in 1960, daily counts of the numbers of flying butterflies were made within the 500 x 800 feet "Lodge Meadow" study area (see Emmel & Emmel, 1962b), which contained 46 species recorded for the Pass (see Table III). This area is composed of both wet and dry meadows. These counts were made by direct observation and represented numbers seen for each species between 10 and 12 a.m. daily. The total number of butterflies recorded in this latter study was 7,720. To determine "success" in *numbers of flying adults,* the daily counts for numbers of individuals for each of the species in a family were added together, and this figure was calculated as a percentage of the total for all families. Thus the contribution of each family toward the composition of the Donner

Pass butterfly fauna can be compared on a percentage basis, both as regards numbers of species and numbers of individuals.

OBSERVATIONS

Some 74 butterfly species were found in the Donner Pass area, and these species belonged to seven of the major families of Rhopalocera found in the western United States. The number of species in each of these groups varied from 1 for the Danaidae to 28 for the Lycaenidae, or in terms of percentage of the total Pass fauna, 1.4% to 37.8% of all the species. Table I shows the composition of the Rhopalocera groups recorded in the *total* Pass area.

Table II and Figure 1 show the composition of the butterfly fauna recorded in *each* of the four general habitats of the Donner Pass area; the figures in Table II represent the per cent of total species in each habitat that belong to each family, while the graphs in Figure 1 show actual number of species for each family in each habitat. It is immediately obvious that the *montane* and *dry-meadow* habitats have the largest faunas of the four areas, and that the Lycaenidae family is usually dominant as regards number of species.

As stated earlier, it was possible to obtain some data on the number of individuals of each species (46 in all) occurring in the Lodge Meadow study area. The composition and relative abundance of the six major Rhopalocera groups recorded there are given in Table III. For the most part, there is a good correlation between number of species and number of individuals for each family.

DISCUSSION AND CONCLUSIONS

The number of butterfly species found in this six-square-mile area of the Sierra Nevada is unusually high. Tilden (1959) records only 43 species as occurring in the Tioga Pass region, representing a study area of approximately the same size although of somewhat higher elevations (over 9941 feet above sea level). Garth (1935) records about 100 species for all of Yosemite National Park (area 1,179 square miles, elevations from 2000 to 13,090 feet), and the present authors and Lloyd M. Martin (personal communication) can note from their experience that the average restricted Sierran locality seems to support around 35 to 65 species. Thus the Donner Pass area is particularly interesting from the standpoint of invesigating the reasons for the occurrence and abundance of a species in a specific habitat, for as noted earlier (Emmel & Emmel, 1962a) this region is a meeting place for a variety of habitats and a high number of plant species, and these factors may be viewed as possible reasons for this variety of Rhopalocera.

The relative proportions in number of species among the Rhopalocera groups involved seems to follow the relative number as found throughout North America north of Mexico (determined from Ehrlich, 1961). The descending order of these groups in terms of number of

TABLE I. Composition of the seven major Rhopalocera groups recorded in the Donner Pass area.

Family	No. of Species	% of Total Species
Papilionidae	5	6.8
Pieridae	8	10.8
Danaidae	1	1.4
Satyridae	2	2.7
Nymphalidae	20	27.0
Lycaenidae	28	37.8
Hesperiidae	10	13.5
TOTALS	74*	100.0%

*In our earlier paper (Emmel & Emmel, 1962a), 74 species and 2 "forms", Anthocaris sara reakirti and Colias eurytheme amphidusa, were listed, making a total of 76 phenotypically-distinct entities.

species is (both in the continent and local Pass faunas): Lycaenidae, Nymphalidae, Hesperiidae, Pieridae, Papilionidae (follows Satyridae in the continent fauna), Satyridae, Danaidae.

However, when the total Pass fauna is divided in terms of occurrence in each of four habitats, patterns of apparent preference for certain habitats emerge — both for all families combined and for individual groups (Table II and Figure 1). The highest total number of species (60) occur in the *montane* habitats, the next highest (55) in the *dry meadow* areas, the third highest (44) in the *wet meadows,* and the lowest number (26) in the forest areas. The descending sequence of environmental support of number of butterfly species is thus:

Montane > Dry Meadows > Wet Meadows > Forest.

This pattern, obtained by comparing numbers of Rhopalocera species, is probably explained by the observed fact that the *montane* areas contained a greater variety of "mico-habitats" than any other area. These micro-habitats included small stream areas, exposed mountain tops, open and brushly talus slopes, etc., ranging from 7100 to 8383 feet in elevation, the greatest range in altitudes for any of the four "macro-habitat" areas considered. Such variation in ecological conditions (especially from edaphic and climatic standpoints) permits a wide variety of potential food plants to flourish. Axelrod (1960) has commented on the marked diversity of habitats in montane areas and the possible influence of this condition on early angiosperm evolution through permitting rapid development and adaptive radiation. Such diversity also influences butterfly distribution, variation, and speciation (see Emmel & Emmel, 1962a; Le Gare & Hovanitz, 1951; Moeck, 1957), and provides potential areas for successful invasion by butterflies already occurring elsewhere.

The large number of total species in the *dry meadow* areas is believed to be due to the great variety of known food plants occurring there; the *wet meadows* supported correspondingly fewer food-plant species. The *forest* areas contained the least variety of micro-habitats and food plants; also, solar radiation, an important influence on butterfly flight habits (see Emmel & Emmel, 1962b), was obviously at a considerably lower level in this habitat than in the other three. Table IV shows the number of known food-plant genera in each habitat for each Rhopalocera group. These and the preceding data agree with the theory that a greater variety in each of these Sierran butterfly groups is more likely to occur where micro-habitats and food plants are most varied, as these conditions, together with a high level of solar radiation, provide support for a wider selection of species than in such areas as pine forests.

This theory can be applied equally to the question of why one group has more species than another group in a certain habitat. The Papilionidae are more successful in forest than in montane areas in terms of per cent of total species there, but they actually have the most species in the latter areas. So we must consider:

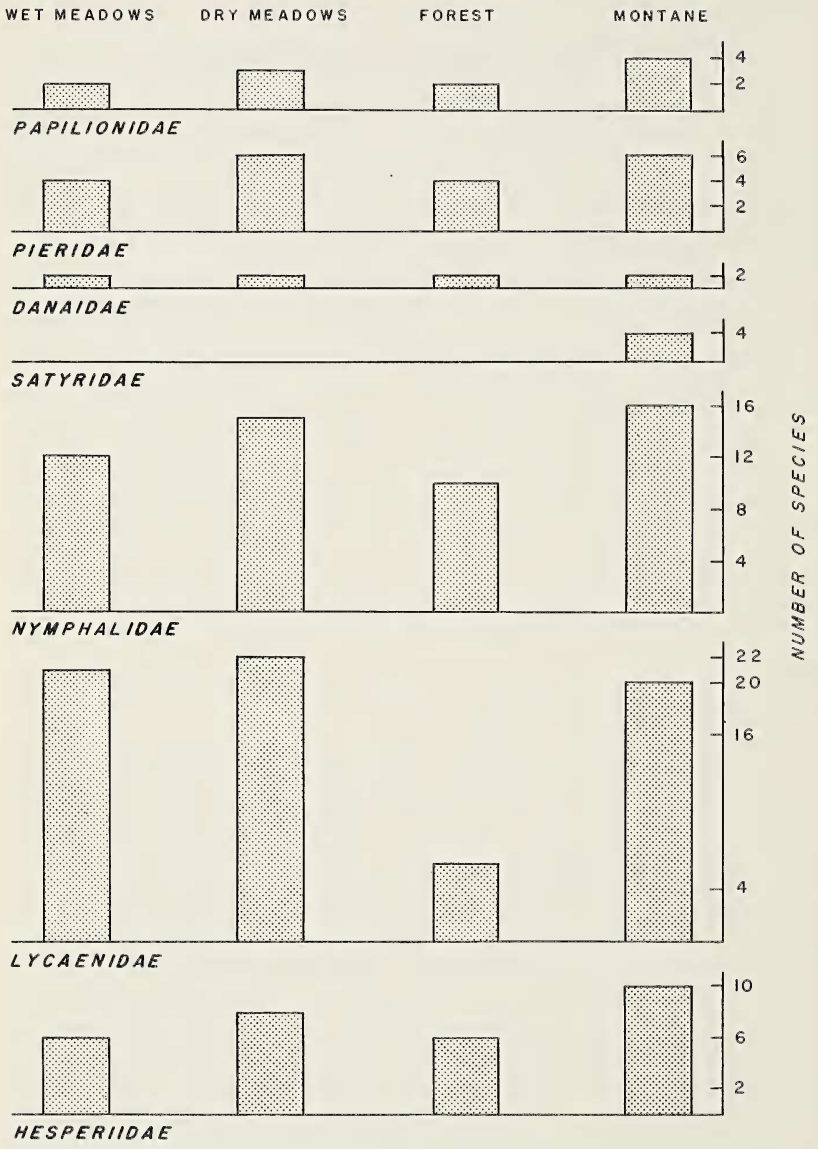

Fig. 1. Numerical composition of the butterfly fauna recorded in each of the four general habitats of the Donner Pass area.

1) That habitat in which the group has its highest *percentage* of the total species population:

Papilionidae	Forest (7.7%)
Pieridae	Forest (15.4%)
Danaidae	Forest (3.8%)
Satyridae	Montane (3.3%)
Nymphalidae	Forest (38.4%)
Lycaenidae	Wet Meadows (45.5%)
Hesperiidae	Forest (19.2%)

2) That habitat in which the group has the most species (direct number):

Papilionidae	Montane (4)
Pieridae	Dry Meadows, Montane (6)
Danaidae	(1 in each habitat)
Satyridae	Montane (2)
Nymphalidae	Montane (16)
Lycaenidae	Dry Meadows (22)
Hesperiidae	Montane (10)

The really significant consideration in evaluating a group's contribution to the fauna in a series of habitats would seem to be the *number* of species it has existing in each habitat. Of course, a further and perhaps more important consideration would be the number of individuals of the group in that habitat, but these data were not obtained. However, speaking from the standpoint of number of species the butterfly groups are uniformly most successful in the montane and dry meadow habitats.

As opposed to evaluating the most suitable habitat for most groups, one can also consider the success of individual groups in colonizing or existing in the various habitats. In the wet meadow, dry meadow, and montane habitats, the Lycaenidae are the most abundant group—with 20 to 22 species in such areas. The Nymphalidae take second place (10 to 16 species) except in the forest zone where they lead the other groups in number of species. The Hesperiidae are third—with 5 to 10 species in each zone—except for being second in the forest areas (leading the Lycaenidae). The Pieridae are uniformly fourth (4 to 6 species) while the Papilionidae have only 2 to 4 species in each zone. There is only one species in the Danaidae (all habitats, however) and two in the Satyridae (montane habitat only).

This apparent relative success of each group, in our opinion, is not due to a "better" adaptation (the result of natural selection) of a group's species in one or another habitat, as Ehrlich (1962) has emphasized. Instead, from our observations, success is likely due to the fact that food plants of species in the seven Rhopalocera families were more varied (as to number of kinds; Table IV), generally more numerous (as to number of individuals of each plant species), and

TABLE II. Composition of the butterfly fauna recorded in each of the four general habitats of the Donner Pass area.*

Family	Habitat Area**			
	Wet Meadows	Dry Meadows	Forest	Montane
Papilionidae	4.5	5.5	7.7	6.7
Pieridae	9.1	10.9	15.4	10.0
Danaidae	2.3	1.8	3.8	1.7
Satyridae	0.0	0.0	0.0	3.3
Nymphalidae	27.3	27.3	38.4	26.7
Lycaenidae	45.5	41.0	15.4	35.0
Hesperiidae	11.4	14.5	19.2	16.7
(1) TOTAL SPECIES	44	55	26	60
(2) PERCENTAGE OF TOTAL PASS FAUNA (74 species) REPRESENTED:	59.5%	74.3%	35.2%	81.1%

*The numbers in each vertical column (file) represent percent of total species in that one habitat (the total number of species is found at the bottom of each column). The actual numbers of species of that family in each habitat, from which the preceding percentages were calculated, are shown in graphic form in Figure 1.

**See Emmel & Emmel (1962a) for map and complete description of all habitats in the Pass area.

more generally distributed for the Lycaenids than for the Nymphalids, for Nymphalids than for Hesperids, etc. It is concluded in this paper that the composition of a butterfly fauna is affected by the requirements (or adaptation) of each butterfly species in that fauna for a certain food plant, in addition to a certain level of solar radiation and other factors as noted in Emmel & Emmel, 1962a. In turn, food plants obviously have grater chances of finding proper environmental conditions in a macro-habitat that contains a number of varied micro-habitats, each with particular edaphic and climatic conditions. The greater the number of host food plants, the greater the number of potentially successful butterfly species, and this theory is believed to account for the observed distribution of the 74 butterfly species (of seven major groups) among the four macro-habitats of the Donner Pass area.

TABLE III. Composition and relative abundance of the six major Rhopalocera groups recorded in the Lodge Meadow habitat.

Family	No. of Species	% of Total Species	% of Total Individuals Recorded
Papilionidae	2	4.4	4.7
Pieridae	4	8.7	9.8
Danaidae	1	2.2	0.3
Nymphalidae	15	32.6	44.9
Lycaenidae	16	34.8	23.2
Hesperiidae	8	17.4	16.7
TOTALS	46	100.1%	99.6%

SUMMARY

1. The Donner Pass area in Placer County, California, supports an extraordinary number (74) of Sierran Rhopalocera species, and its varied habitats and vegetational associations make the area particularly interesting for investigating the basis for the occurrence and abundance of a species and a family in a specific habitat.

2. The number of species in the seven major families of the Pass area are proportionately equivalent to the numbers of species in these

TABLE IV. Number of known food plant genera in each habitat for each Rhopalocera family*

Rhopalocera Family	Habitat Area			
	Wet Meadows	Dry Meadows	Forest	Montane
PAPILIONIDAE	Salix	--	Ceanothus	Cymopterus Salix (stream) Ceanothus Prunus Sedum
PIERIDAE	Cruciferae genera Trifolium	Cruciferae genera Trifolium	Pinus	Cruciferae genera
DANAIDAE	--	--	--	--
SATYRIDAE	(Grasses)	(Grasses)	(Grasses)	Grasses
NYMPHALIDAE	Viola Castilleia Salix Plantago	Castilleia Aster Cirsium Ribes Gnaphalium Lupinus	Ceanothus	Castilleia Aster Chrysopsis Ceanothus Salix (stream) Lupinus
LYCAENIDAE	Salix Lupinus Trifolium Potentilla	Ceanothus Lupinus Polygonum Ribes Eriogonum Potentilla Calyptridium Trifolium	Arceuthobium Pinus	Ceanothus Lupinus Polygonum Sedum Eriogonum Astragalus
HESPERIIDAE	Potentilla Grasses Sidalcea?	Potentilla Grasses Sidalcea	--	Potentilla Grasses

*Data summarized from text of Emmel & Emmel, 1962a.

groups as found for the whole of North America (north of Mexico). From most to least number of species: Lycaenidae, Nymphalidae, Hesperiidae, Pieridae, Papilionidae (follows Satyridae for North American fauna), Satyridae, Danaidae.

3. The highest total number of butterfly species in Donner Pass occurs in the *montane* habitats (60 species). The *dry meadow* habitats support 55 species, the *wet meadow* habitats have 44 species, and the *forest* areas have 26 species occurring in them.

4. The basis of this distribution is explained by the theory that a greater food-plant diversity occurs in the areas (such as the montane macro-habitats) that have a number of micro-habitats, each with particular edaphic and micro-climatic conditions, and that this host-plant diversity promotes the immigration and continued successful existence of more Rhopalocera species than in less diversified macro-habitats (such as these Sierran forest habitats). The possible influence of such factors as solar radiation and climate acting directly on butterflies rather than plants is also considered.

5. Data obtained on the number of flying individuals of all species found in the Lodge Meadow area showed there was usually a good correlation between number of species and number of individuals for each family in this restricted Sierran locality.

SYSTEMATIC LIST OF RHOPALOCERA OCCURRING AT DONNER PASS, PLACER COUNTY, CALIFORNIA

PAPILIONIDAE
1. *Papilio zelicaon* Lucas
2. *Popilio indra indra* Reakirt
3. *Papilio rutulus* Lucas
4. *Papilio eurymedon* Lucas
5. *Parnassius clodius baldur* Edwards

PIERIDAE
6. *Neophasia menapia* Felder & Felder
7. *Pieris sisymbrii* Boisduval
8. *Pieris protodice* Linnaeus
9. *Pieris rapae* Linnaeus
10. *Euchloe creusa hyantis* Edwards
11. *Anthocaris sara* form *julia* Edwards
12. *Colias eurytheme* Boisduval
13. *Colias philodice eriphyle* Edwards

DANAIDAE
14. *Danaus plexippus* Linnaeus

SATYRIDAE
15. *Ceononympha tullia californica* Westwood
16. *Cercyonis sthenele oetus* Boisduval

NYMPHALIDAE
17. *Speyeria cybele leto* Behr
18. *Speyeria zerene zerene* Boisduval
19. *Speyeria coronis snyderi* Skinner
20. *Speyeria atlantis irene* Boisduval
21. *Speyeria mormonia arge* Strecker
22. *Boloria epithore* Edwards
23. *Chlosyne palla* Boisduval
24. *Chlosyne hoffmanni hoffmanni* Behr
25. *Phyciodes campestris montana* Behr
26. *Phyciodes mylitta* Edwards
27. *Polygonia zephyrus* Edwards
28. *Nymphalis californica* Boisduval
29. *Nymphalis milberti* Latreille
30. *Nymphalis antiopa* Linnaeus
31. *Vanessa cardui* Linnaeus
32. *Vanessa atalanta* Linnaeus
33. *Vanessa virginiensis* Drury
34. *Vanessa carye* Hubner
35. *Precis lavinia* Cramer
36. *Limenitis lorquini* Boisduval & Leconte

LYCAENIDAE
37. *Satyrium californica* Edwards
38. *Satyrium sylvinus* Boisduval
39. *Satyrium saepium* Boisduval
40. *Satyrium behrii* Edwards
41. *Satyrium fuliginosa* Edwards
42. *Strymon melinus* Hubner
43. *Callophrys johnsoni* Skinner
44. *Callophrys nelsoni* Boisduval

45. *Callophrys augustinus iroides* Boisduval
46. *Callophrys eryphon* Boisduval
47. *Callophrys dumetorum perplexa* Barnes & Benjamin
48. *Lycaena arota virginiensis* Edwards
49. *Lycaena editha* Mead
50. *Lycaena nivalis* Boisduval
51. *Lycaena cupreus* Edwards
52. *Lycaena heteronea* Boisduval
53. *Everes comyntas amyntula* Boisduval
54. *Plebejus anna* Edwards
55. *Plebejus saepiolus* Boisduval
56. *Plebejus icarioides* Boisduval
57. *Plebejus shasta* Edwards
58. *Plebejus acmon* Westwood & Hewitson
59. *Plebejus (acmon?) lupini* Boisduval
60. *Agriades glandon podarce* Felder & Felder
61. *Glaucopsyche lygdamus behrii* Edwards
62. *Philotes enoptes* Boisduval
63. *Philotes battoides intermedia* Barnes & McDunnough
64. *Celastrina argiolus echo* Edwards

HESPERIIDAE

65. *Thorybes nevada* Scudder
66. *Pyrgus ruralis* Boisduval
67. *Pyrgus communis* Grt.
68. *Erynnis juvenalis* Fabricus
69. *Erynnis afranius* Lint.
70. *Hesperia juba* Scudder
71. *Hesperia nevada* Scudder
72. *Hesperia harpalus* Edwards
73. *Polites sonora* Scudder
74. *Polites sabuleti tecumseh* Grin.

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